

SEASONAL VARIATION IN NEST PLACEMENT BY THE CALIFORNIA GNATCATCHER

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ABSTRACT.—Nest placement of open-nesting bird species may affect risk of nest predation, nest microclimate, and reproductive success. In populations that breed in multiple habitat types and over long seasons, nest placement should vary seasonally and by habitat to compensate for seasonally changing and habitat specific environmental conditions that might affect the relationship between nest placement and reproductive success. Using data collected during 1994 and 1995, I investigated seasonal and habitat specific patterns of nest placement in a population of California Gnatcatchers (*Polioptila californica*) that breeds over a 5 month period. Nest and substrate (plant in which nest is built) height increased and vegetative concealment of nests decreased seasonally, but these variables were not related to habitat type. Substrate height varied with substrate species in 1994, and use of individual substrate species varied seasonally. Reproductive phenology differed between the two major habitat types used by gnatcatchers in this study. Whether these seasonal and habitat specific changes in nest placement are adaptive responses to changing environmental conditions that may affect reproductive success has yet to be determined. Received 15 Feb. 2000, accepted 11 June 2000.

In open nesting birds, variation in nest placement may affect predation risk (Best and Stauffer 1980, Wilcove 1985, Martin 1988, 1993, Morton et al. 1993; Sockman 1997; but see Filliater et al. 1994) and nest microclimate (Walsberg and King 1978, Walsberg 1981; but see Walsberg 1985). In populations that breed in multiple habitats and over long seasons, nest placement should vary seasonally and by habitat to compensate for seasonally changing and habitat specific environmental conditions that may affect the relationship between nest placement and reproductive success.

The California Gnatcatcher (*Polioptila californica*) is an open nesting, non-migratory passerine that lives in the coastal sage scrub ecosystem of southern California. Its nesting season may last at least 5 months (Sockman 1997), a period over which ambient temperature and precipitation vary considerably (Fig. 1). Its range extends from the Pacific Coast to more than 100 km inland (Atwood 1980) and subsumes several habitat types. Here, I present data on its nest height, height and species of the nest substrate (plant in which the nest is built), and vegetative concealment of nests and how they change with habitat type and phenology of clutch initiation.

METHODS

This study was conducted at Naval Air Station Miramar in San Diego County, California. I have depicted the study site and distribution of breeding pairs previously (Sockman 1997, fig. 1). The site covers approximately 9,600 ha of hilly terrain with several extensive canyons and ridges and extends approximately 20 km from east to west. Elevation ranges from 80–330 m. Dominant habitat types occupied by gnatcatchers are chaparral and coastal sage scrub, which together cover approximately 60% of the site (J. F. O'Leary, unpubl. data).

Data were collected from mid-March to early August in 1994 and 1995, covering the period from the earliest egg-laying to the completion (fledging) of the last known nest each season. Nests were found by searching suitable habitat and by observing birds approach or leave nests. I attempted to find at least one nest of as many pairs as possible throughout the study site and seasons. Nest distribution was fairly uniform across the entire study site and similar between the two years (see Sockman 1997, fig. 1).

I determined the date of clutch initiation in nests found during laying by back calculating using the number of eggs in the nest (laid one per day). I determined date of clutch initiation in nests found during incubation by waiting until eggs hatched and back calculating using a 14 day incubation period (Sockman 1997) and the number of eggs in the nest. I determined date of clutch initiation in nests found with nestlings by estimating the age of nestlings and back calculating as described above. A few nests found during incubation were abandoned before hatching occurred. For these, I could not determine date of clutch initiation, but I used data from these nests when date of clutch initiation was not included in an analysis.

Once laying was completed, I recorded the nest's height (measured from the ground directly below the nest to the bottom of the nest), substrate height (mea-

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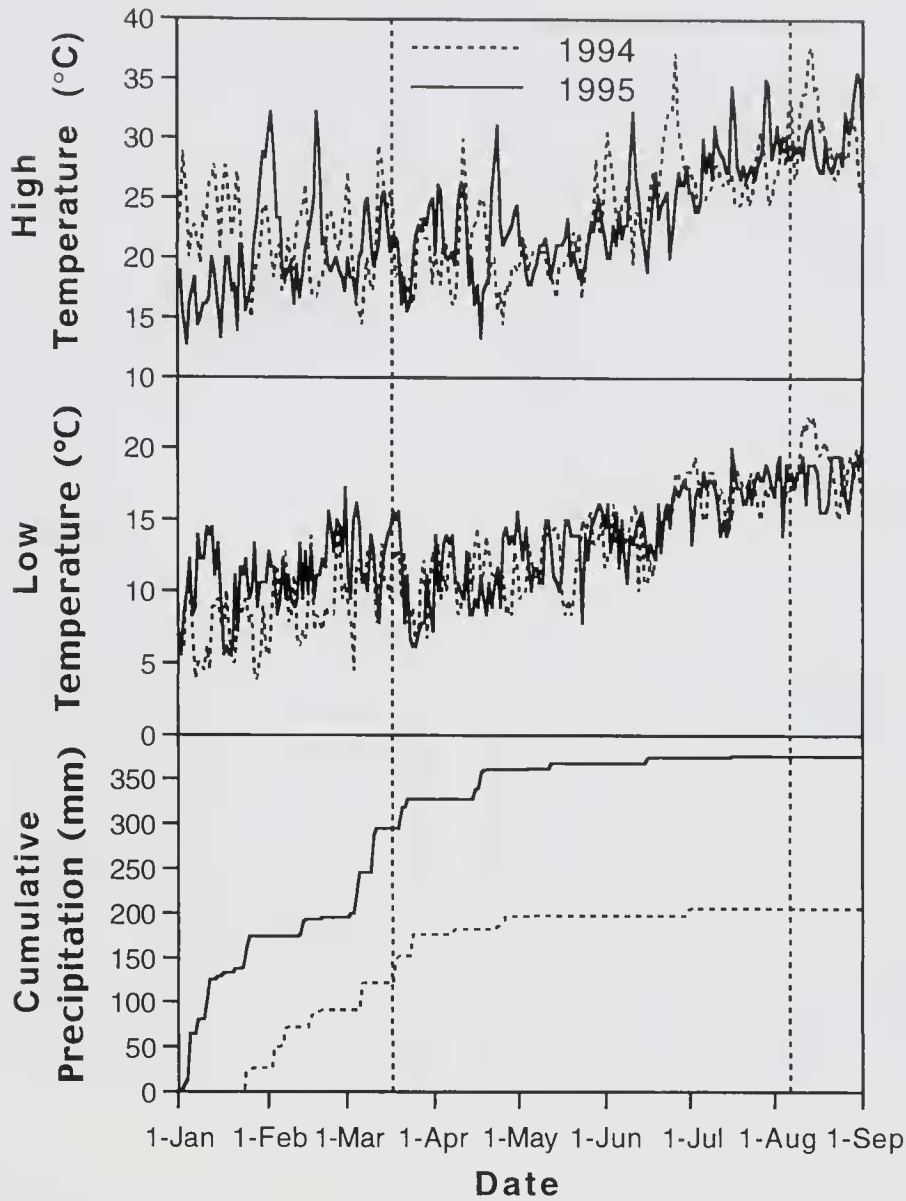


FIG. 1. Daily high and low temperatures and cumulative daily precipitation at Naval Air Station Miramar, San Diego County, California. Vertical, dashed lines delineate the nesting season for California Gnatcatchers.

sured from the ground directly below the nest to the highest point of the shrub within a 30 cm horizontal radius of the nest), lateral vegetative concealment (percent of the nest laterally obscured by vegetation at nest level averaged over estimates from the north, south, east, and west sides 1 m from the nest), and vegetative concealment from above (percent of the nest obscured by vegetation when viewed from 1 m directly above the nest). Because nearly all nests were relatively low and in short substrates, I collected data without the need for a ladder or mirror. Nests were often located on steep slopes and I could view even the few high nests from directly above by standing uphill. I defined relative nest height as the ratio of the nest height to the substrate height and nest ceiling as the difference between substrate height and nest height.

I assigned nests to one of two topographically defined habitat sub-types (arroyo and upland) and recorded the nest substrate species. Both arroyo and upland are sub-types of the coastal sage scrub habitat. I

defined arroyos as those areas within the flood plain of ephemeral waterways (i.e., these were the bottoms of canyons). I defined upland as those areas corresponding to the sides of these canyons or to mesas above such canyons. The primary rationale for distinguishing between the two habitat sub-types (hereafter habitats or habitat types) was their profound qualitative difference in plant-species composition. The arroyos were dominated by *Baccharis sarothroides* and the uplands by plant species typical of coastal sage scrub, including *Artemisia californica*, *Eriogonum fasciculatum*, *Salvia mellifera*, *Salvia apiana*, and others. Although each species was sometimes found in either habitat, the two habitats differed markedly in species composition, and I analyzed only nests that I could unambiguously assign to one of the habitats. Temperatures and precipitation were recorded from central locations on the study site (see Sockman 1997).

To maximize the statistical independence among sampling units, I analyzed one nest per breeding pair.

randomly selecting one when multiple nests per pair per year were available. Thus, analyses are not necessarily conducted with first nests of a pair. For statistical analyses, I used SuperANOVA 1.11 (Abacus Concepts, Inc., Berkeley, California), Excel 98 (Microsoft Corporation, Redmond, Washington), and StatView 5.0 (SAS Institute, Inc., Cary, North Carolina), each for the Macintosh. I used a contingency table analysis to determine if frequency of substrate species use differed between years. The distributions of each dependent variable used in the parametric statistical analyses described below did not significantly differ from normal (Kolmogorov-Smirnov Tests for Normality of Distribution: $P > 0.05$ for each test). I analyzed each of the two years separately and used two MANCOVA models (for each year) to determine how nest height, substrate height, and vegetative concealment varied seasonally and with respect to habitat type. Nest height, relative nest height, nest ceiling, and substrate height were dependent variables in the first model, and lateral vegetative concealment and vegetative concealment from above were dependent variables in the second. Date of clutch initiation (covariate), habitat type, and their interaction were independent variables for both models. The interaction term was not statistically significant in these models and was therefore removed from the analyses. I used ANOVA to determine whether variation in date of clutch initiation (dependent variable) was explained by habitat type (independent variable).

I used additional analyses to examine the relationships among significantly related variables in the above multivariate analyses. I regressed substrate height, nest height, and lateral vegetative concealment individually on date of clutch initiation. I used an ANOVA model to determine how the date of clutch initiation (dependent variable) varied according to substrate species (independent variable), a MANOVA model to determine how substrate height and nest height (dependent variables) varied according to substrate species (independent variable), and an ANOVA model to determine how lateral vegetative concealment (dependent variable) varied according to substrate species (independent variable). In analyses with substrate species as a variable, I included only those species used as nest substrates at least five times and used Fisher's protected least significant difference for post-hoc analyses. I report both multivariate Wilks' λ P values and P values from univariate tests.

RESULTS

I used 107 nests in analyses, 58 from 1994 and 49 from 1995 [not all nests were used in all analyses (see Methods)]. Breeding pairs were widely distributed across the study area and were generally associated with major canyons. Clutch-initiation dates of randomly selected nests ranged from 18 March–3 July.

In arroyos, gnatcatchers initiated clutches

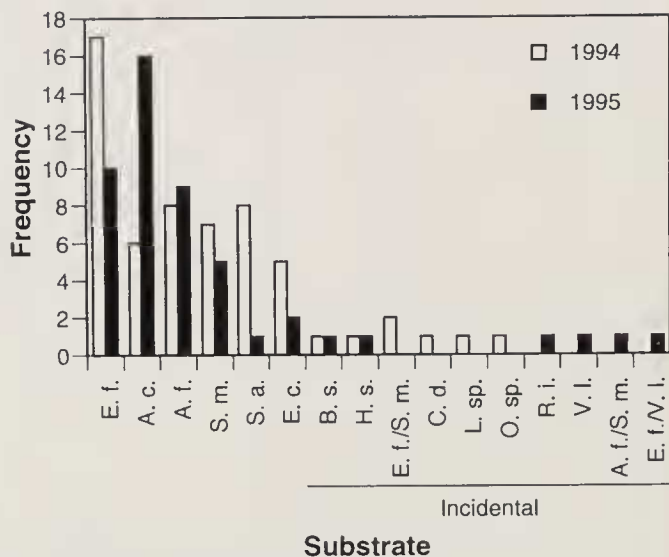


FIG. 2. Frequencies of nest substrates in the California Gnatcatcher. For statistical comparison between 1994 and 1995 frequencies, a substrate with fewer than 5 nesting events for 1994 and 1995 combined was termed "incidental" and excluded. E. f. = *Eriogonum fasciculatum*, A. c. = *Artemisia californica*, A. f. = *Adenostoma fasciculatum*, S. m. = *Salvia mellifera*, S. a. = *Salvia apiana*, E. c. = *Eriodictyon crassifolium*, B. s. = *Baccharis sarothroides*, H. s. = *Haplopappus squarrosus*, E. f./S. m. = *Eriogonum fasciculatum*/*Salvia mellifera* complex, C. d. = *Cneuridium dumosum*, L. sp. = *Lonicera* sp., O. sp. = *Opuntia* sp., R. i. = *Ribes indecorum*, V. l. = *Viguiera laciniata*, A. f./S. m. = *Adenostoma fasciculatum*/*Salvia mellifera* complex, E. f./V. l. = *Eriogonum fasciculatum*/*Viguiera laciniata* complex.

[1994: $\bar{x} = 16$ Apr ± 6.19 days (SE), $n = 18$; 1995: $\bar{x} = 13$ Apr ± 6.53 days, $n = 8$] approximately 2 weeks earlier on average than in upland habitat (1994: $\bar{x} = 2$ May ± 5.17 days, $n = 37$; 1995: $\bar{x} = 4$ May ± 4.38 days, $n = 40$). The difference was marginally significant in both years (ANOVA: 1994: $F_{1,53} = 3.74$, $P = 0.058$; 1995: $F_{1,46} = 4.38$, $P = 0.042$). Note that these analyses were not conducted exclusively with each pair's first nest but rather with a randomly selected nest from each pair when more than one per pair were available.

Gnatcatchers nested in a variety of shrub species (Fig. 2), but some species, notably *Eriogonum fasciculatum* and *Artemisia californica*, were used substantially more frequently than others. If incidental (occasionally used) species (shrubs nested in fewer than five times in 1994 and 1995 combined) were excluded, gnatcatchers showed a shift in substrate use from 1994 to 1995 (Contingency Table Test: $\chi^2 = 16.26$, 5 df, $P = 0.006$).

Each year, nest height, substrate height, relative nest height, and nest ceiling combined in a multivariate analysis were related to date of clutch initiation (MANOVA: 1994: Wilks' $\lambda F_{4,49} = 4.46, P = 0.004$; 1995: Wilks' $\lambda F_{4,42} = 2.67, P = 0.045$) but not to habitat type (MANOVA: Wilks' $\lambda P > 0.05$ for each year). Inspection of the univariate statistics indicated that in each year substrate height (ANOVA: 1994: $F_{1,52} = 13.50, P < 0.001$; 1995: $F_{1,45} = 6.51, P = 0.014$) and nest height (ANOVA: 1994: $F_{1,52} = 14.74, P < 0.001$; 1995: $F_{1,45} = 7.22, P = 0.01$) significantly increased with date of clutch initiation (Fig. 3) but relative nest height and nest ceiling did not (ANOVA: $P > 0.05$ for each variable in each year).

Each year, lateral vegetative concealment and vegetation concealment from above combined in a multivariate analysis were related to date of clutch initiation (MANOVA: 1994: Wilks' $\lambda F_{2,51} = 5.45, P = 0.007$; 1995: Wilks' $\lambda F_{2,44} = 6.38, P = 0.004$) but not to habitat type (MANOVA: Wilks' $\lambda P > 0.05$ for each year). Univariate statistics indicated that lateral vegetative concealment declined (ANOVA: 1994: $F_{1,52} = 6.36, P = 0.015$; 1995: $F_{1,45} = 12.32, P = 0.001$) and vegetative concealment from above did not change (ANOVA: 1994: $F_{1,52} = 2.15, P > 0.05$; 1995: $F_{1,45} = 0.90, P > 0.05$) with date of clutch initiation (Fig. 3).

To further assess the relationships among those variables that showed significant relationships in the above multivariate analyses, I regressed substrate height, nest height, and lateral vegetative concealment individually on date of clutch initiation. Each year, date of clutch initiation explained a small but statistically significant percentage of variation in substrate height (Linear Regression: 1994: $F_{1,53} = 11.82, P = 0.001, R^2 = 0.18$; 1995: $F_{1,46} = 5.26, P = 0.026, R^2 = 0.10$), nest height (Linear Regression: 1994: $F_{1,53} = 13.53, P < 0.001, R^2 = 0.20$; 1995: $F_{1,46} = 5.22, P = 0.027, R^2 = 0.10$), and lateral vegetative concealment (Linear Regression: 1994: $F_{1,53} = 5.54, P = 0.022, R^2 = 0.10$; 1995: $F_{1,46} = 9.74, P = 0.003, R^2 = 0.18$). The curvilinear appearance of nest height plotted against date of clutch initiation (Fig. 3) suggested that some of these regressions may be better described by quadratic than by linear equations. The addition of a date² term to the linear re-

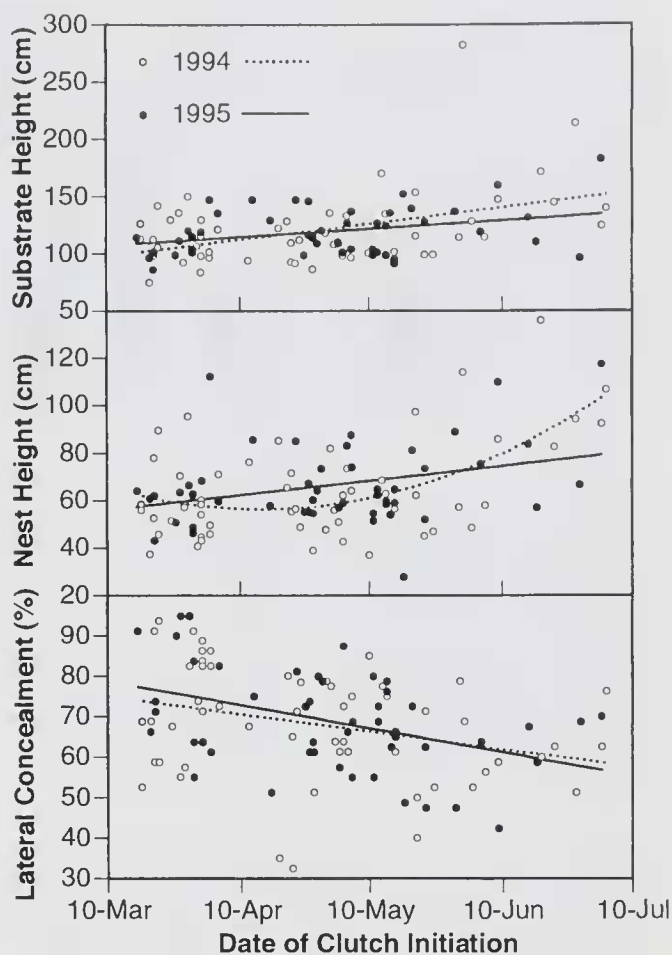


FIG. 3. Change in substrate height, nest height, and lateral vegetative concealment with respect to date of clutch initiation in nests of the California Gnatcatcher.

gressions above resulted in a significant improvement of the fit of the regression model for 1994 nest height (Multiple Regression: $F_{2,52} = 11.99, P < 0.001, \text{adjusted } R^2 = 0.29$) but not for any of the other regressions (Fig. 3).

If nest placement varied with substrate species and use of substrate species varied seasonally, then seasonally changing nest-placement characteristics might be caused by a seasonal shift in substrate species. To examine this, I analyzed the relationships between substrate species and date of clutch initiation, between substrate species and each of substrate height and nest height, and between substrate species and percent lateral concealment. Each year (ANOVA: 1994: $F_{4,39} = 2.96, P = 0.031$; 1995: $F_{3,36} = 3.10, P = 0.039$), gnatcatchers built nests in *Adenostoma fasciculatum* significantly later than in other plant species (Fig. 4). In 1994, both substrate height (ANOVA: $F_{5,45} = 10.98, P < 0.001$) and nest height

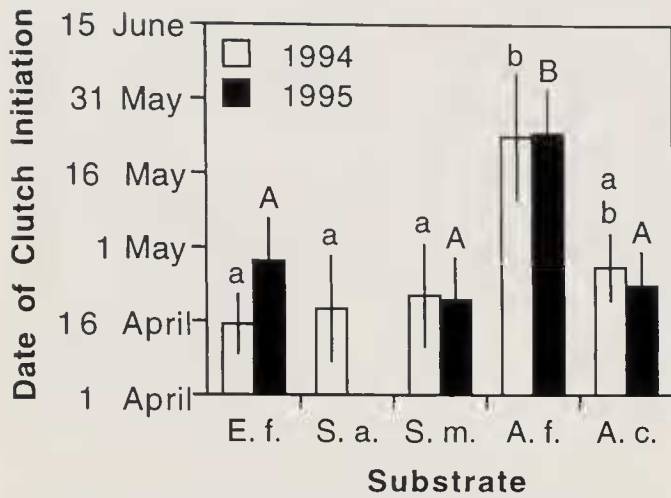


Fig. 4. Change in date of clutch initiation (mean \pm 1 SE) with respect to nest substrate species in California Gnatcatchers. Abbreviations are defined and samples sizes shown in Fig. 2. Species used as a substrate fewer than five times (i.e., *Salvia apiana* in 1995) were excluded from this analysis. Within a year, species without a letter in common were significantly different ($P < 0.05$) based on post-hoc analyses.

(ANOVA: $F_{5,45} = 5.10$, $P < 0.001$) were related to substrate species (MANOVA: Wilks' $\lambda F_{10,88} = 4.81$, $P < 0.001$). These relationships were primarily because *A. fasciculatum* was a taller substrate than other species and because nests built in *A. fasciculatum* were higher than those built in other substrates (Fig. 5). In 1995, the relationship between substrate species and substrate and nest height was not significant (MANOVA: Wilks' $\lambda P > 0.05$). In neither year was lateral vegetative concealment significantly related to substrate species (ANOVA: 1994: $F_{5,45} = 2.05$, $P > 0.05$; 1995: $F_{3,36} = 1.70$, $P > 0.05$).

DISCUSSION

Over two approximately 16-week clutch initiation seasons, California Gnatcatchers built nests in a variety of plant species, similar to findings previously published for this species (Grishaver et al. 1998). Nest height, substrate height, and vegetative concealment varied seasonally, but I could not determine whether this reflected a seasonal change in choice or in availability of nest sites. Braden (1999) found that nest placement in California Gnatcatchers is not random with respect to the concealment or species of substrates, suggesting that nest-site selection is not entirely based on availability of sites. Still, I cannot rule out the possibility that seasonal changes in avail-

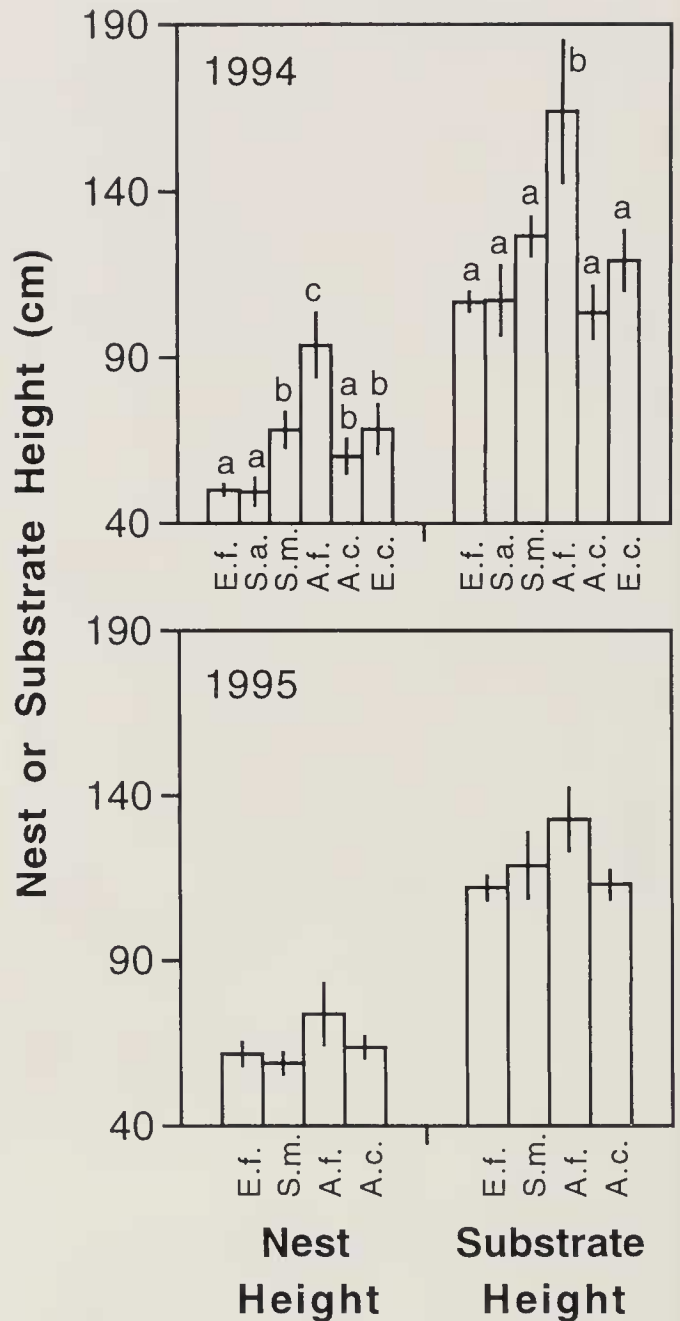


FIG. 5. Change in nest and substrate height (mean \pm 1 SE) with respect to substrate species in California Gnatcatchers. Abbreviations are defined and samples sizes shown in Fig. 2. Species used as a substrate fewer than five times (i.e., *Salvia apiana* in 1995) were excluded from this analysis. Species without a letter in common were significantly different ($P < 0.05$) based on post-hoc analyses.

ability of sites gave rise to the seasonal changes in nest placement I observed.

The finding that date of clutch initiation differed between habitats (although only marginally) is similar to previous findings in which gnatcatcher nesting phenology depended on habitat characteristics such as grass and forb cover and increased number of perennials (Braden et al. 1997). I did not quantify habi-

tat-specific differences in vegetative characteristics, but qualitative differences in species composition between the two habitat types were profound and may have given rise to the differing phenologies of clutch initiation. In successive nesting attempts, individual pairs would sometimes move from arroyo to adjacent upland, suggesting that perhaps the differing phenology of nest initiation was not due to a difference between birds nesting in arroyo versus upland.

Adenostom fasciculatum was used as a nest substrate later in the season and, in 1994, was taller than other substrates. This raises the possibility that the 1994 seasonal increase in substrate height was a consequence of a seasonal shift in substrate species. The same logic applies to the seasonal increase in nest height, in that nest height in 1994 was also higher in *A. fasciculatum* than in other substrate species. However, in 1995 substrate height and nest height were not related to substrate species and both substrate height and nest height still increased. This indicates that, at least in some cases, substrate and nest height increase seasonally and independently of seasonal changes in substrate species.

Variation in nest placement affects the probability of nest predation in the California Gnatcatcher (Sockman 1997). Risk of nest predation does not change seasonally and is greatest in the lowest and highest nests and smallest in those nests built in the middle range of nest heights (Sockman 1997). Consequently, minimizing the risk of nest predation alone would not explain the seasonal increase in nest height, but it is possible that seasonal changes in nest height minimize risk of nest predation to the extent that other factors potentially important in nest placement, such as nesting microclimate, are not compromised.

With spring growth, the foliage of coastal sage scrub becomes denser from early spring through summer. If nests were built randomly with respect to concealment, I would predict a seasonal increase in vegetative concealment. I also expected late-season nests to be more concealed than those built early because of the seasonal increase in ambient temperature (Fig. 1) and the fact that, in some species, concealment may affect the nest's microclimate (Walsberg 1985). Previously (Sockman 1997),

I found no evidence that variation in vegetative concealment affected nest predation. One possible explanation for the finding that concealment did not increase seasonally is that gnatcatchers seasonally modify nest placement and, in doing so, avoid seasonal increases in nest concealment. It is likely that gnatcatchers position nests in response to factors other than microclimate or risk of nest predation, such as ease of parental access.

Nest site selection in open nesting birds has probably evolved under the collective influence of many factors. In environments where the risk of nest predation is high, optimal nest placement can make the difference between reproductive success and several weeks of wasted time and energy (Best and Stauffer 1980; Wilcove 1985; Martin 1988, 1993; Sockman 1997). Additionally, the inability of eggs and newly hatched altricial nestlings to thermoregulate makes the placement of the nest in an optimal microclimate critical for parents that must balance energetic constraints between time spent on and time spent off the nest (Walsberg 1985). If the tolerance for variation in microclimate is low and risk of nest predation is high, then the fluctuation of climatic and predator regimens expected to occur over a relatively long season should produce commensurate changes in nest placement. The temporal extent of this study (2 5-mo nesting seasons) provided a potentially strong framework for investigating temporal dynamics of nest placement. However, only a small fraction of the variation in nest placement was explained by season, suggesting that other variables may be important.

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